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From genome to wheat: Emerging opportunities for modelling wheat growth and development

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Abstract

Ecophysiological models of crop growth and development sometimes show unrealistic responses that are attributable to our incomplete understanding of the processes the models attempt to describe. Rapid advances in plant genetics, genomics and biochemistry offer important opportunities for improving representations of key processes of growth and development. Research on incorporation of genetic information in models supports this potential, especially in modelling cultivar performance across environments. This paper reviews progress in using information from genetics, genomics and allied fields in modelling and examines approaches suitable for modelling wheat (*Triticum aestivum* L. and *T. durum* Desf.). Efforts to model wheat crops should first focus on the relatively well-understood genetic systems affecting phenology and plant height. A simple gene-based approach using linear equations to estimate cultivar-specific parameters has the advantage that it can easily be implemented in existing wheat models. One requirement is to integrate data on the genetic makeup of wheat cultivars with results from field trials that can be used to estimate genetic effects and evaluate model performance. Concomitantly, modellers should exploit findings from genomics and allied fields on wheat and other plant species in order to improve sub-models of individual processes, using more complex representations of gene action. Advances in these more mechanistic representations require much more detailed and quantitative studies on how gene action varies with specific environmental signals such as temperature and photoperiod.

Keywords: Genomics; Vernalization; Photoperiod; Growth habit; Photoperiod

1. Introduction

Crop simulation models are widely used in agricultural research as tools to examine complex interactions of environment, management and cultivar. Such models are only as accurate as the descriptions of the processes they attempt to describe and integrate. Not surprisingly, while the qualitative responses of models usually are sound and quantitative predictions are reasonable for common production situations, model performance often proves problematic for extreme environments, for complex traits such as grain quality, and for novel cultivar-types. Arguably, representations of ecophysiological processes in crop models have advanced little since the late 1970s and early 1980s when many basic principles of plant ecophysiology were first established and incorporated into such models (e.g., Wit, 1978; Loomis and Connor, 1992).

Advances in plant genetics, genomics and biochemistry suggest various opportunities for strengthening ecophysiological models. These include both through better understanding of the control of physiological processes and from improved characterization of genetic differences among lines and cultivars. Several recent papers illustrate this potential (Hoogenboom and White, 2003; Stewart et al., 2003; Welch et al., 2003; Messina et al., 2006) or present detailed arguments for potential benefits of applying genomic research and allied fields to modelling (Tardieu, 2003; White and Hoogenboom, 2003; Baenziger et al., 2004; Yin et al., 2004; Wollenweber et al., 2005).

Wheat science has seen important advances in sequencing and characterizing of major gene loci. Two of the loci for reduced plant height, *Rht-B1* and *Rht-D1*, were sequenced and shown to be homologous to the *Gibberellin Insensitive* (*GAI*) locus in *Arabidopsis thaliana* (Peng et al., 1999). The wheat vernalization gene *Vrn-A1* is similar to *APETALA1* in Arabidopsis (Yan et al., 2003). Other examples include the "*T. aestivum heading*" (*TaHd1*; Nemoto et al., 2003) and *Vrn-A2* (Yan et al., 2004a) loci. An intensive effort is underway to sequence and characterize the *Ppd* loci that control photoperiod response (Laurie et al., 2004), and considerable progress has been made in understanding the molecular regulation of wheat grain hardness and protein concentration (Giroux and Morris, 1998; Giroux et al.,

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2000; See et al., 2004), and seed weight (Smidansky et al., 2002). It is timely to inquire whether wheat is a suitable target for gene-based modelling and if so, what approaches are most appropriate for developing gene-based wheat models.

This paper reviews different approaches for incorporating information from conventional genetics and from genomics and associated fields into crop models and then suggests strategies for applying these approaches to wheat modelling. The terminology surrounding genomics and related fields such as "proteomics", "transcriptomics", "metabolomics" and even "phenomics" is somewhat confusing, so the term "plant biology" is used for endeavours that range from the study of the plant genome, genomics, to plant biochemistry.

2. Approaches for applying plant biology in ecophysiological models

Various approaches can be envisaged for applying plant biology in crop models. These parallel the three highest levels of genetic detailed found in crop models as identified by White and Hoogenboom (2003; Table 1). The first two approaches that are discussed here, gene- and QTL-based modelling, correspond mainly to level 4, with potential for implementation at level 5. The third approach, application of plant biology, mainly concerns level 5 but can involve any of the levels. The fourth, modelling networks of genes, proteins and other molecules, is the realm of "systems biology" and corresponds to level 6.

2.1. Gene-based modelling

Models that simulate ecotype or cultivar differences for traits such as phenology, partitioning and yield components typically use cultivar-specific parameters. Such parameters are often referred to as "genetic coefficients", but they are usually determined empirically through calibrations using phenotypic data. Examples include coefficients for potential development rate (or its equivalent in thermal time) and reference values of grain number and size, which may be used to estimate rates of increase in grain number and grain size with adjustments for assimilate supply or other factors. An obvious application of plant biology is in estimating such parameters using data for actual genotypes of lines or cultivars, but plant biology can also identify new genes and provide insights into action of specific genes or gene networks.

Table 1
Six levels of genetic detail in crop simulations models

(1) Generic, no specific crop or species identified. Modelled responses are assumed similar across species, or they only describe differences among major functional types
(2) Species-specific, no cultivars. Differences among species are modelled, but genetic differences among cultivars or lines (e.g., in phenology, growth rate or growth habit) are not considered
(3) Cultivar differences represented by quantitative model parameters. Genetic differences among cultivars or lines are represented through quantitative parameters such as for photoperiod sensitivity, potential developmental rates, and reference leaf area and grain weights
(4) Cultivar differences represented by genotypes with linear effects on model parameters. Genetic differences among cultivars or lines are represented through linear effects on model parameters affecting traits such as photoperiod sensitivity, potential developmental rates, and reference leaf area and grain weights
(5) Cultivar differences expressed through processes described using knowledge of gene expression and gene products. Differences among cultivars or lines are represented through switches affecting specific processes such as stem elongation or photoperiod effects on reproductive development
(6) Full representation of gene regulators, gene-products, etc. in networks. Plant growth or development is described by scaling up from information on gene-sequences or at least, specific gene-products using methods of systems biology

The GeneGro model (White and Hoogenboom, 1996) simulated effects of seven genes in common bean (*Phaseolus vulgaris* L.), using the BEANGRO model (Hoogenboom et al., 1994) as the foundation. Genetic effects were incorporated by estimating the cultivar-specific parameters used in BEANGRO (e.g., for photoperiod sensitivity or characteristic-specific leaf area) with linear models representing additive and epistatic gene effects. A cultivar that was homozygous dominant at a gene locus was assigned a value of 1, and if recessive, a value of 0. GeneGro simulated growth and development as well as BEANGRO (White and Hoogenboom, 1996), but GeneGro specified cultivar differences with only seven binary coefficients, the seven loci, that could be determined without field calibration data.

When tested with an independent set of data representing 14 trials and 39 cultivars (a total of 213 treatment combinations), GeneGro explained 75% of variation in days to flowering, 68% in days to maturity, 39% of in seed mass and 11% in seed yield (Hoogenboom et al., 1997). Regression analyses indicated that the model explained a much large portion of variation ($P < 0.01$) when differences in mean yields of trials were accounted for (Table 7 of Hoogenboom et al., 1997). Although not examined in their paper, 17 of the cultivars which were simulated were not used to develop or calibrate the model. Thus, GeneGro successfully simulated performance of new genotypes in new environments and can be said to partially explain genotype × environment interactions for phenology and seed yield.

GeneGro was subsequently adapted to the cropping system model (CSM; Jones et al., 2003), being released as CSM-GeneGro-Drybean (Hoogenboom et al., 2004), and the approach was successfully extended to prediction of phenology in soybean (Messina et al., 2006). Examples of the equations used to estimate cultivar coefficients in GeneGro are given in Table 2. Selection of the independent variables was guided by information on gene function and action, with the final selection depending on standard statistical tests for stepwise regression. Thus, since the *Ppd* and *Hr* loci interact (show epistasis) in their effect on photoperiod sensitivity (Kornegay et al., 1993), the equation for relative response of reproductive development to photoperiod included effects of both loci plus an interaction term (Table 2).

2.2. QTL-based modelling

Identifying individual major genes for physiological traits still remains difficult (Edmeades et al., 2004), and the low num-

Table 2
Examples of genetic effects used to estimate ecotype or cultivar coefficients in the CSM-GeneGro-Drybean model

Cultivar parameter	Linear model of genetic effects	R^2
Relative response of reproductive development to photoperiod	PPSEN = 0.004 + 0.0154 × *Ppd* + 0.036 × *Hr* − 0.0104 × *Ppp* × *Hr*	0.66
Time between plant emergence and flower appearance	EM-FL = 26.63 + 4.886 × *Fin* − 5.188 × *Fd*	0.58
Time between first flower and end of leaf expansion	FL-LF = 18.0 + 3.8 × *Fd* − 6.9 × *Ssz-2*	0.61
Specific leaf area under standard growth conditions	SLAVR = 322 + 41 × *Ssz-1* − 38.0 × *Ssz-2* − 25.3 × *Ssz-2*	0.49
Average seed per pod under standard growing conditions	SDPDVR = 5.14 − 0.2 × *Fin* − 1.9 × *Ssz-1* + 0.24 × *Ssz-3*	0.98
Maximum ratio of seed over pod weight at maturity	THRSH = 78 − 3.5 × *Ssz-2* + 1.5 × *Fin* × *Ssz-2*	0.75
Maximum weight per individual seed	WTPSD = 0.22 + 0.21 × *Ssz-1* + 0.07 × *Ssz-2*	0.90

Genes are coded as 1 for homozygous dominant and 0 for homozygous recessive at each locus. The *Ppd* and *Hr* loci condition photoperiod sensitivity, *Fin* gives an indeterminate growth habit, *Fd* decreases time to flowering, and the three *Ssz* loci affect seed size (White and Hoogenboom, 1996; Hoogenboom et al., 2004).

ber of known loci severely constrains gene-based modelling. Even when appropriate phenotyping procedures and parental materials are available, an inheritance study with requisite populations of progenies may require multiple years to execute. Molecular tools can facilitate hypothesis generation and confirmation of inheritance patterns (e.g., Sourdille et al., 2002), but they do not eliminate the need for creating segregating populations and for precision phenotyping (Campos et al., 2004). In the absence of information on classical genetic loci, quantitative trait loci (QTLs) can be used to characterize lines or cultivars. To identify QTLs, the positions of molecular or other genetic markers are determined along chromosomes by analysing recombination patterns. Individual markers are associated with quantitative traits using various statistical procedures, the loci showing the strongest associations being the QTLs (Tanksley, 1993; Kearsey and Farquhar, 1998). In applications to simulation modelling, model parameters are the quantitative traits. QTLs are identified for each parameter and then used to estimate parameter values in a manner similar to that used in the gene-based approach (White and Hoogenboom, 1996).

Gene-based and QTL approaches overlap depending on how strongly a QTL is associated with a classical locus. The three, hypothetical seed size loci considered in GeneGro (White and Hoogenboom, 1996) were inferred mainly from previous QTL studies (Vallejos and Chase, 1991). In the QTL-based model of Yin et al. (2000a), discussed below, the accuracy of the model was partially attributable to the large effects of the *Denso* locus, which is a classical locus that affects growth habit and phenology (Yin et al., 1999).

Yin et al. (2000a) modelled barley (*Hordeum vulgare* L.) growth and development using QTLs by estimating ten model coefficients of the SYP-BL model. This model is based on routines from the SUCROS and ORYZA1 models and quantifies barley growth and development by integrating leaf photosynthesis to the canopy scale on a daily basis (Yin et al., 2000b). The QTL version of the model predicted shoot biomass and yield with an accuracy similar to SYP-BL, although both models performed poorly with validation data sets. This work has recently been extended to modelling phenology (Yin et al., 2005), and a similar approach was successfully applied to flowering response of rice (*Oryza sativa* L.; Nakagawa et al., 2005). In both cases, the QTL-based models were able to predict phenology in a new environment, although the tests were limited to the calibration set of inbred lines.

An ecophysiological model for leaf expansion in maize (*Zea mays* L.) was used by Reymond et al. (2003) to analyse the genetic variability for responses to temperature and water deficit. Coefficients for a series of response curves for elongation rate were related to QTLs obtained from a population of 100 recombinant inbred lines. For validation data for 13 lines grown under six regimes, the model accounted for 74% of variation in elongation rate. QTLs have also been used in static models of plant morphology (Buck-Sorlin and Bachman, 2000). Increasingly, it appears that the QTL-based modelling will work best for analysing traits that are more fundamental or processes that are either stable across environments or show readily quantifiable responses, for example, phenology as affected by temperature and photoperiod.

While QTL-based modelling has value for analysing specific traits or processes, the approach shares difficulties inherent in all QTL analyses (Kearsey and Farquhar, 1998). Although basic approaches for QTL identification are straightforward, many studies do not consider possible interactions among loci (epistasis). Validation and evaluation of genetic and environmental dependencies of QTL action are demanding tasks. Detection of false positives among candidate markers is especially problematic, and large population sizes (e.g., >250 individuals or lines) are recommended to detect QTLs reliably (Charmet, 2000; Hackett, 2002; Bernardo, 2004; Schon et al., 2004). Most QTL analyses are based on populations derived from biparental crosses, so the selection of the parents determines the range of genetic variation detectable in the test material. Association mapping, which uses lines, cultivars or germplasm accessions, may alleviate some of these constraints (Gebhardt et al., 2004; Kraakman et al., 2004) but still requires phenotypic data from large numbers of entries and has other constraints (Jannink and Walsh, 2002).

2.3. Plant biology

Modelling based on plant biology includes traditional plant physiology but implies use of genomics, transcriptomics and related fields as additional sources of information. Plant biology extends into all aspects of plant growth and development, and for any process considered in a plant simulation model, there likely is applicable information emerging from studies on the molecular biology of Arabidopsis, rice or other plant species. Journals such as *Annual Review of Plant Biology*, *Current Opinion in*

Plant Biology and *Trends in Plant Science* are excellent sources of review papers. The discussion below briefly illustrates applications of plant biology to modelling photosynthesis and cold tolerance. Examples related to phenology and growth habit are explored later.

Photosynthesis is an especially attractive target for application of plant biology since the biochemistry and genetics have been extensively studied. Detailed models of the biochemical pathways have a long history (e.g., Hahn, 1987). However, new information is emerging from studies of gene-expression and responses of lines with specific mutations or gene-insertions (e.g., Kramer et al., 2004; Pfannschmidt, 2003), suggesting modifications to existing models as well as ways to validate models more rigorously. For example, Poolman et al. (2000) described a model of 18 enzymes of the Calvin–Benson cycle and found that the predicted relative influence of different enzymes were consistent with studies of transgenic plants.

The Farquhar–von Caemmerer photosynthesis model (Farquhar et al., 1980) is widely used in crop modelling. It provides a level of process detail that is simpler than full models but mechanistically represents interacting effects of temperature, irradiance and concentrations of CO_2 and O_2. One simplification is the assumption that rubisco activation does not limit photosynthesis. Crafts-Brandner and Salvucci (2004) reviewed various lines of evidence, including mRNA and protein abundance, and concluded that the activation state of rubisco, which is regulated by the activity of rubisco activase, does limit photosynthesis at elevated temperatures and CO_2 concentrations. Collatz et al. (1991) described a modification to the Farquhar–von Caemmerer photosynthesis model where rubisco activation is diminished at higher temperatures. Thus, information from molecular studies provided support for a previously suggested modification.

Cold acclimation is an induced plant response that is of particular relevance to wheat production. Studies with Arabidopsis established that CBF/DREB1genes are upregulated by cold treatments and that their products activate a range of cold-responsive (*Cor*) genes (Thomashow, 1999, 2001). Wheat is now known to have various *Cor* genes (e.g., Ohno et al., 2001; Takumi et al., 2003). Fowler et al. (1999) combined evidence from conventional genetic and molecular studies on cold acclimation to modify the CERES-Wheat model by including a cultivar-specific factor LT50, which represents the crown temperature at which 50% of the population is killed. This approach merits revisiting to see whether information at the molecular level can be used to refine the acclimation and dehardening responses assumed to affect LT50 in CERES-Wheat.

2.4. "Systems biology" and regulatory networks

Given complete sequence data for the genome of a crop, a long-term research goal would be to infer the major metabolic pathways and their regulation and thus, to deduce the agricultural characteristics of the crop. With information on sequence differences among lines or cultivars, optimal sequence combinations could be predicted for a specific production situation. Plant systems biology seeks to build from bioinformatics to develop techniques for modelling how networks of genes and gene products interact (Blanchard, 2004). "The 2010 Project" thus proposes to model a virtual plant based on the genomic description of Arabidopsis (Chory et al., 2000). Minorsky (2003) reviews the numerous methodological challenges, including new tools for data management, high throughput imaging systems for analysing large protein complexes, tools for visualizing the concentration of specific metabolites in sub-cellular compartments and ultimately, software to dynamically model processes from sub-cellular to whole plant levels that involve complex and often redundant networks of pathways.

The term "systems approach" is invoked as if a systems perspective was new to biology (e.g., Ideker et al., 2001), but this perspective was central to early work in ecological simulation, including for crops and agricultural systems (e.g., Wit, 1978). The key difference is that previous efforts have considered process scales from the community or whole plant levels downward while plant systems biology proposes to move from the genome level upward. Hammer et al. (2004) discuss these contrasting approaches to scale of process and conclude that greater progress requires much more dialogue between systems biology and ecophysiological modelling. This argument was echoed by Edmeades et al. (2004) for broader application of plant biology to field-level physiology.

Current models in systems biology focus mainly on single organelles or cells or specific processes or developmental events. E-Cell is a simulation environment for modelling organelles or cells (Takahashi et al., 2002, 2004). E-Cell was used to model 14 enzymes of photorespiration, considering three cellular components, chloroplasts, peroxisomes and mitochondria (Dhar et al., 2001). This work is being extended to a complete plant cell (Wang, 2002). The section for the Calvin–Benson cycle considers 39 metabolites and 32 reactions, and various strategies for the light reactions are under review. Welch et al. (2003, 2004) modelled phenology of Arabidopsis using a genetic neural network and in an independent set of over 100 observations mainly from the literature, the model explained about 74% of variation in total leaf number. While plant systems biology is attracting attention, it is too early to judge how tractable the basic research problems, data management and complex simulations will prove and thus, what contributions the field will make to crop modelling in coming years.

3. Towards gene-based modelling of wheat

Considering the different approaches for introducing genetic information into wheat models, there is a trade-off between simple methods based on conventional genetics versus pursuit of plant systems biology. Simple approaches offer concrete prospects of progress, while systems biology holds more exciting promise but perhaps is years off from simulating whole plants, much less crops species growing in realistic field conditions. Thus, I suggest we commence efforts to develop a new generation of wheat models by making full use of known genes and concomitantly, seeking answers through

plant science to resolve questions that prove recalcitrant using traditional field and laboratory approaches. The basic feasibility of simple approaches is supported by previous work with common bean and soybean. For wheat, availability of data on genotypes and field performance is still a potential limitation, so data availability is reviewed in the next two sections.

3.1. Availability of genetic data for wheat

Numerous major loci for physiological traits are known for wheat (Table 3), so wheat does appear amenable to gene-based modelling. Genes controlling photoperiod sensitivity, vernalization, earliness per se and stem height in wheat are understood well enough to permit simulating their effects in exploratory efforts. Additional genes, including ones for frost tolerance, grain size, protein concentration and osmoregulation, also merit consideration. One notes, however, the apparent scarcity of information on genes affecting processes such as photosynthesis, respiration and root–shoot partitioning. This may reflect either that these processes are affected by large networks of genes, each gene having a relatively minor effect, or that accurate characterization of genotypes has impeded gene discovery.

A logical first step toward a gene-based model is to characterize the genetic makeup (alleles present for major loci) of diverse wheat cultivars from different sets of field trials. Data can be extracted from published lists (e.g., McIntosh et al., 2003; van Beem et al., 2005), databases (Martynov et al., 2002) and expert opinion. Over the next 5 years, however, rapid genotyping with molecular tools should become routine. "Perfect" markers are available for the *Rht-B1b* and *Rht-D1b* loci (Ellis et al., 2002), and reliable markers are available for the *Vrn-1* loci (Sherman et al., 2004; Yan et al., 2004b) and the *PinA-D1* and *PinB-D1* loci (Morris et al., 2001).

3.2. Availability of field data for wheat

Gene-based modelling also requires access to a large assemblage of phenotypes, crop management and environments for wheat lines tested under a wide range of conditions. Access to such data could be greatly facilitated through collaborative efforts to exchange data in common formats. The Global Change

Table 3
Examples of loci of potential interest for developing gene-based wheat models

Locus	Function	Key references
Phenology		
Eps-A1a	Earliness per se	Miura et al. (1999); Shah et al. (1999)
Eps-Am1	Thermo-sensitive earliness per se	Bullrich et al. (2002)
Vrn-A1, *Vrn-B1*, *Vrn-D1*	Dominant for spring growth habit (reduced vernalization)	Yan et al. (2003, 2004b)
Vrn-A2	Dominant for winter habit	Yan et al. (2004a)
Ppd-A1, *Ppd-B1*, *Ppd-D1*	Insensitive to short days	Laurie et al. (2004)
TaHd1-1, *TaHd1-2*, *TaHd1-3*	Photoperiod response	Nemoto et al. (2003)
Growth habit or morphology		
Rht-B1, *Rht-D1*	Reduced plant height	Worland et al. (1998); Ellis et al. (2002); Ahmad and Sorrells (2002)
Tin	Tiller inhibition	Richards (1988); Duggan et al. (2002)
Hd, *B1*, *B2*	Dominant inhibitor of awns	Sourdille et al. (2002)
Hl1, *Hl2*	Hairy leaf	Taketa et al. (2002)
W1, *W2*, *W1I*, *W2I*, *W3I*	Glaucousness due to epicuticular waxes	Tsunewaki and Ebona (1999)
Grain quality		
R-A1, *R-B1*, *R-D1*	Seed dormancy associated with red pigment (phenolics) in seed	Flintham and Humphray (1993)
Phs	Pre-harvest sprouting, seed dormancy	Flintham et al. (2002)
Pro1, *Pro2*	Grain protein content	Law et al. (1978)
Gpc-6B1	Increased grain protein content in durum wheat	Khan et al. (2000)
Pina-D1, *Pinb-D1*	Grain hardness, weight and protein concentration	Giroux and Morris (1998); Morris et al. (2001)
Various physiological traits		
Nra	Nitrate reductase activity	Gallagher et al. (1980)
Or	Osmotic adjustment	Morgan and Tan (1996); Blum et al. (1999)
Fr1, *Fr2*	Frost tolerance	Snape et al. (1997)
Mineral nutrition		
ALMT1	Aluminum tolerance through an Al activated malate transporter	Sasaki et al. (2004)
Bo1, *Bo2*, *Bo3*	Tolerant to high levels of boron	Paull et al. (1991)
Bod1, *Bod2*	Boron efficiency (tolerates low B levels in soil)	Jamjod et al. (2004)
Cdu1	Low cadmium uptake	Penner et al. (1995)
Ce	Copper efficiency (tolerates low Cu in soil)	Graham et al. (1987); Schlegel et al. (1991)
Kna	Potassium vs. sodium discrimination	Dubcovsky et al. (1996)

Further references are found in McIntosh et al. (2003).

and Terrestrial Ecosystems (GCTE) Focus 3 Wheat Network developed a common set of data for wheat modelling using the draft standards of the International Consortium for Agricultural Systems Applications (Hunt et al., 2001). Phenotypic data for hundreds of wheat yield trials coordinated by CIMMYT are available in electronic format (Payne et al., 2002), but data on management and environments for these trials are currently too incomplete for effective modelling. Data from studies using sets of near-isogenic lines would be especially useful but again, have not been compiled for modelling.

3.3. Moving from data to models

Once data on genetic makeup of specific lines or cultivars are in hand and are associated with phenotypic data from field trials, cultivar parameters have to be estimated from a diverse set of trials using appropriate methods for a given model. With data on genotypes and cultivar parameters in hand, equations for estimating the parameters as function of genotypes can be estimated using multiple linear regressions as described for GeneGro or more advanced techniques. The resulting equations can either be coded into a specific model (as done in GeneGro) or implemented through an external, stand-alone coefficient estimator. The latter approach appears especially desirable since it permits modellers to explore gene-based approaches without modifying model source code. One coefficient-estimating tool could provide cultivar inputs for various models. Of course, as new genetic information is incorporated through revision of modelled processes, the cultivar parameters used as inputs would have to be re-calibrated and the estimation process repeated.

4. Applying plant biology to wheat modelling

While developing gene-based wheat models using data for known loci, researchers should also seek to increase use of process-level knowledge obtained from plant biology. One goal would be to replace individual linear equations for gene effects with more process-based representations. Greater emphasis is needed on clarifying details of processes that have proven recalcitrant using traditional research approaches. Control of flowering provides several instructive examples that are discussed below in the context of a qualitative model for growth and partitioning specified using a Forrester diagram (Fig. 1; Forrester, 1961). Photoperiod and vernalization processes are assumed to affect a developmental rate that, in turn, controls partitioning of assimilate to reproductive and vegetative biomass. This diagram differs little from those used to describe standard crop models (e.g., Penning de Vries et al., 1989) except that development rate is explicitly influenced by levels of separate photoperiod and vernalization signals, which are influenced by the alleles present at the *Ppd* and *Vrn* loci.

A first question for plant biology is what mechanisms cause temperature to affect the photoperiod response of wheat. Interactions of vernalization with photoperiod response are known for wheat (e.g., Flood and Halloran, 1986; González et al., 2002) and in other crops, photoperiod sensitivity increases with temperature (e.g., White et al., 1996; Yan and Wallace, 1998). A direct temperature effect would require linking temperature to the photoperiod response valve of Fig. 1, possibly involving a different temperature than used for vernalization (e.g., foliage versus shoot apical). Alternatively, the photoperiod by temperature interaction may occur at the stage of signal integration (see

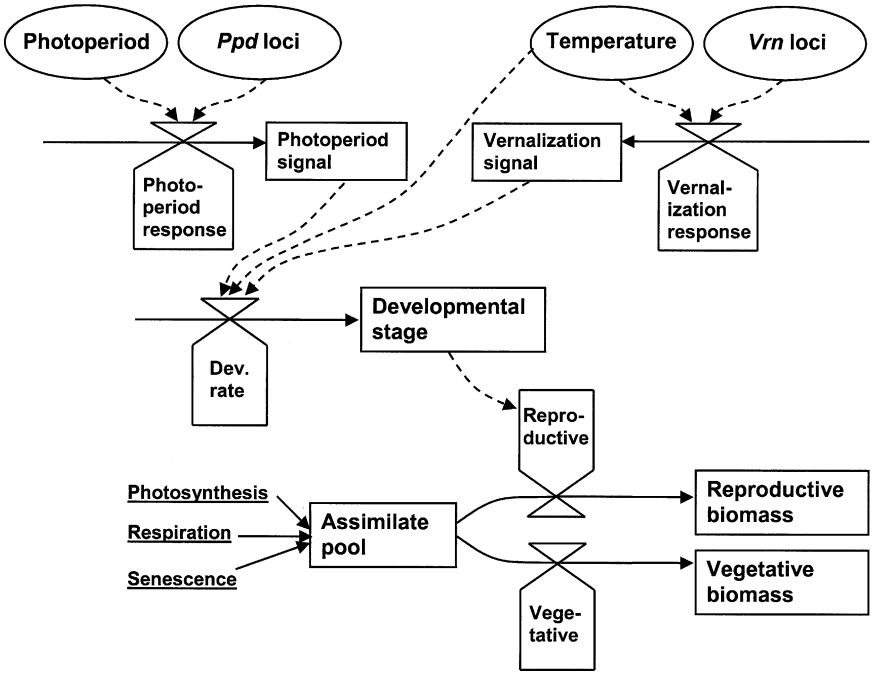

Fig. 1. Conceptual model for control of reproductive partitioning in wheat using notation of Forrester (1961). Boxes are state variables; valves are control flows; ellipses are auxiliary variables; solid lines are flows of material; dashed lines are flows of information; underlined variables would be input from other sections of a complete plant growth model.

Fig. 1). In this case, there is no need to incorporate a direct link between temperature and the photoperiod response valve but to change the integration of signals model to a multiplicative model as used in CROPGRO. An interaction with vernalization would likely require a link between the photoperiod and vernalization response valves. With the current capacity to quantify levels of mRNA from vernalization loci, one starting point might be to test the proposal of Stefany (1993) that the vernalization requirement in wheat determines the length of the juvenile (photoperiod insensitive) phase.

Regardless of whether temperature interacts with photoperiod response, monitoring activity of vernalization genes in different tissues might clarify where the vernalization signal is sensed and thus which tissue temperature is most relevant for quantifying vernalization. Most studies cite the shoot apex as the site of perception of vernalization temperature, but work in Arabidopsis suggests that the *Vernalization Insensitive 3* (*VIN 3*) locus is active both in shoot and root meristems (Fig. 2 of Sung and Amasino, 2004). This partially coincides with the proposal of McMaster et al. (2003) that the phyllochron interval may vary not only with ccrownanopy temperature but also with temperatures of intercalary meristems in internodes and leaf sheaths.

Work with the diploid wheat *Triticum monococcum* showed that *Vrn-A^m-1* is the orthologue of APETALA1 (Yan et al., 2003) and that this gene is upregulated by vernalization. Subsequent work confirmed that *Vrn-A1*, *Vrn-B1* and *Vrn-D1* have very similar (homologous) gene sequences (Yan et al., 2004b). Given these similarities in sequence and function, the assumption implicit in Fig. 1 is that the effect of these loci can be represented by a single influence. Data from Halloran (1967) for chromosome substitution lines reveal an almost linear effect of the dosage of the dominant *Vrn-1* loci on final leaf number (Fig. 2), although there is still a minor genome effect ($P < 0.05$, full ANOVA, data not shown). Although less well studied, the three wheat *Ppd* loci are thought to be homologous (Laurie et al., 2004), so their effect is also simulated through a single process. Using molecular markers such as those available for *Vrn-1*

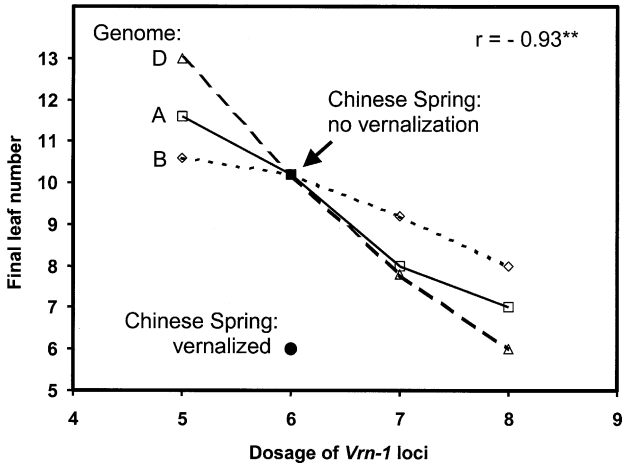

Fig. 2. Relation between final leaf number and dosage of *Vrn-1* loci obtained through aneuploid lines of cv. Chinese Spring. All lines are unvernalized except for one treatment of euploid (normal) Chinese Spring. Based on data from Halloran (1967). The correlation excludes vernalized Chinese Spring.

Table 4
Examples of reported effects of the *Rht-B1* and *Rht-D1* loci on traits in wheat

Trait	Effect of dominant *Rht* alleles	References
Internode lengths	Reduced	Miralles et al. (1998)
Cell length (not width)	Decreased	Miralles et al. (1998)
Leaf blade and sheath length	Reduced	Miralles et al. (1998)
Assimilate partitioning to ear	Increased	Borrell et al. (1993)
Development	Variable	Gale and Youssefian (1985)
Seedling vigour	Decreased	Trethowan et al. (2001)
Harvest index	Increased	Borrell et al. (1993)
Kernel size, weight	Decreased	Miralles et al. (1998)
Root length	Increased	Miralles et al. (1997)
Root length density	No effect	Miralles et al. (1997)
Photosynthesis	Increased	LeCain et al. (1989); Morgan et al. (1990); Watanabe et al. (1994)
Water use efficiency	Variable	Ehdaie and Waines (1996)
Radiation use efficiency	Increased	Miralles and Slafer (1997)

(Sherman et al., 2004), it should be straightforward to test the relative effect of different loci. Efforts to model near-isogenic lines varying for the *Lr19* gene showed unexpected, large effects of genetic background (Hunt et al., 2003), so effect of genetic background should also be considered.

The pleiotropic effects of various wheat *Rht* loci (Table 4) provide an interesting contrast to control of phenology. Rather than having apparently specific switch-like effects over time and in specific tissues, constitutive expression of the *Rht* loci affects not only internode length but numerous other traits (Gale and Youssefian, 1985). For *Rht-B1* and *Rht-D1*, these effects are through loss of responsiveness to gibberellic acid, which plays an important role in cell elongation. The two loci are homologous to the *GAI* locus in *Arabidopsis thaliana*, suggesting that the pleiotropic effects of the two loci can be partially analysed through comparison with effects of *GAI*. Interestingly, however, while *GAI* delays flowering relative to *gai* in Arabidopsis, studies in wheat usually indicate minimal effect of the *Rht* loci on phenology (Gale and Youssefian, 1985).

5. Conclusions

Applying gene-based approaches to wheat modelling offers various avenues for enhancing prediction of how genotype, management and environment interact to affect crop growth and development. Ultimately, this work should lead to increased productivity and decreased negative impacts on the natural resource base, including through greenhouse gas production. Initial benefits of gene-based modelling will largely come through improved characterization of differences among lines or cultivars. Information on patterns of inheritance and on qualitative mechanisms of gene regulation can guide model development. Plant biology is already elucidating details of genetic control of flowering, plant height and photosynthesis that can be applied in crop models.

Modellers and crop physiologists, however, must be proactive in accessing and applying information emerging from plant

biology. Due to the need for data for a diverse set of lines tested in a wide range of environments, success also depends on better integration of large sets of genetic data for individual lines with field evaluation data.

Assuming the various research and logistic issues are resolved sufficiently to permit rapid advances, a fundamental question that remains to be answered is how accurately will gene-based wheat models describe crop performance? Specifically, will the effort invested result in models that are substantially more accurate than current models? With our present understanding of genetic control of physiological traits in wheat, differences among major cultivar groups, as defined by differences among the known or presumed *Vrn-1*, *Ppd* and *Eps* loci (Table 3), should be easily modelled. Further effort should be able to resolve ecotypic differences related to other major genes in Table 3. How much additional progress is possible will depend on yet unresolved issues such as how to accelerate the discovery and characterization of physiologically useful genes and ultimately, how to model action of perhaps hundreds of minor genes which interact through complex networks.

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